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PII: S0377-8398(09)00072-3
DOI: doi: 10.1016/j.marmicro.2009.06.005
Reference: MARMIC 1285

To appear in: *Marine Micropaleontology*

Received date: 4 December 2008
Revised date: 28 May 2009
Accepted date: 19 June 2009

Please cite this article as: Pike, Jennifer, Crosta, Xavier, Maddison, Eleanor J., Stickley, Catherine E., Denis, Delphine, Barbara, Loïc, Renssen, Hans, Observations on the relationship between the Antarctic coastal diatoms Thalassiosira antarctica Comber and Porosira glacialis (Grunow) Jørgensen and sea ice concentrations during the Late Quaternary, *Marine Micropaleontology* (2009), doi: 10.1016/j.marmicro.2009.06.005

Observations on the relationship between the Antarctic coastal diatoms *Thalassiosira antarctica* Comber and *Porosira glacialis* (Grunow) Jørgensen and sea ice concentrations during the Late Quaternary

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ABSTRACT

The available ecological and palaeoecological information for two sea ice-related marine diatoms (Bacillariophyceae), *Thalassiosira antarctica* Comber and *Porosira glacialis* (Grunow) Jørgensen, suggests that these two species have similar sea surface temperature (SST), sea surface salinity (SSS) and sea ice proximity preferences. From phytoplankton observations, both are described as summer or autumn bloom species, commonly found in low SST waters associated with sea ice, although rarely within the ice. Both species form resting spores (RS) as irradiance decreases, SST falls and SSS increases in response to freezing ice in autumn. Recent work analysing late Quaternary seasonally-laminated diatom ooze from coastal Antarctic sites has revealed that sub-laminae dominated either by *T. antarctica* RS, or by *P. glacialis* RS, are nearly always deposited as the last sediment increment of the year, interpreted as representing autumn flux. In this study, we focus on sites from the East Antarctic margin and show that there is a spatial and temporal separation in whether *T. antarctica* RS or *P. glacialis* RS form the autumnal sub-laminae. For instance, in deglacial sediments from the Mertz Ninnis Trough (George V Coast) *P. glacialis* RS form the sub-laminae whereas in similar age sediments from Iceberg Alley (Mac.Robertson Shelf) *T. antarctica* RS dominate the autumn sub-lamina. In the Dumont d'Urville Trough (Adélie Land), mid Holocene (Hypsithermal warm period) autumnal sub-laminae are dominated by *T. antarctica* RS whereas late Holocene (Neoglacial cool period) sub-laminae are dominated by *P. glacialis* RS. These observations from late Quaternary seasonally laminated sediments would appear to indicate that *P. glacialis* prefers slightly cooler ocean-climate conditions than *T. antarctica*. We test this relationship against two down-core Holocene quantiative diatom abundance records from Dumont d'Urville Trough and Svenner Channel (Princess Elizabeth Land) and compare the results with SST and sea ice concentration results of an Antarctic and Southern Ocean Holocene climate similation that used a coupled atmosphere-sea ice-vegation model forced with orbital parameters and greenhouse gas concentrations. We find that abundance of *P. glacialis* RS is favoured by higher

winter and spring sea ice concentrations and that a climatically-sensitive threshold exists between the abundance of *P. glacialis* RS and *T. antarctica* RS in the sediments. An increase to >0.1 for the ratio of *P. glacialis* RS:*T. antarctica* RS indicates a change to increased winter sea ice concentration (to >80% concentration), cooler spring seasons with increased sea ice, slightly warmer autumn seasons with less sea ice and a change from ~7.5 months annual sea ice cover at a site to much greater than 7.5 months. In the East Antarctic sediment record, an increase in the ratio from <0.1 to above 0.1 occurs at the transition from the warmer Hypsithermal climate into the cooler Neoglacial climate (~4 cal kyr) indicating that the ratio between these two diatoms has the potential to be used as a semi-quantitative climate proxy.

Key words: East Antarctica, Quaternary, diatoms, sea ice

1. Introduction

Most of the ecological and palaeoecological information available for sea ice-related marine diatoms *Thalassiosira antarctica* and *Porosira glacialis* suggests that these two species have similar sea surface temperature (SST), sea surface salinity (SSS) and sea ice proximity preferences and similar seasonal occurrences (summarised in Sections 1.1 and 1.2). For example, in Ross Sea surface waters that emerge from beneath the ice shelf, *T. antarctica* cells are associated with a diatom assemblage that also includes *P. glacialis* and *P. pseudodenticulata* (Cunningham and Leventer, 1998). Along the Mac.Robertson Shelf in Iceberg Alley (Figure 1) deglacial seasonally laminated sediments contain abundant *P. glacialis* resting spores (RS) that are found within *T. antarctica* RS-dominated sub-laminae that were deposited during autumn (Stickley et al., 2005). On the other hand, in Dumont d'Urville Trough, Adélie Land (Figure 1), sub-laminae dominated by *T. antarctica* RS are found in mid-Holocene (relatively warm, Hypsithermal) laminated sediments (Core MD03-2601, Denis et al., 2006), whereas sub-laminae dominated by *P. glacialis* RS are

found in late Holocene (cool, Neoglacial) sediments (Core MD03-2597, Maddison, 2006). Further, deglacial/early Holocene laminated sediment from Mertz Ninnis Trough, George V Coast (Figure 1), also contain sub-laminae dominated by *P. glacialis* RS (Maddison et al., 2006). The *T. antarctica* RS and *P. glacialis* RS sub-laminae from both sites, and from both time intervals, occur at the top of late summer/autumn terrigenous-rich diatom laminae, which supports the contention that these two diatoms have broadly similar ecological preferences (Stickley et al., 2005). However, as pointed out by Denis et al. (2006), the more coastal position of the Mertz Ninnis Trough and MD03-2597 core sites (and associated *P. glacialis* RS sub-laminae) compared to the core site MD03-2601 (and associated *T. antarctica* RS sub-laminae) suggests that *P. glacialis* prefers cooler temperatures with higher sea ice concentrations than *T. antarctica*. In this study we review the available ecological information for these two diatom species. We then consolidate the perceived relationship between the two taxa as sedimentary indicators of autumnal conditions using laminated sediment sequences and published ecological information. Finally, we investigate down-core Holocene diatom assemblage records from two sites in coastal East Antarctica in order to establish whether the relationship developed from laminated sediment records and ecological information can be used as a more quantitative proxy for changing environmental conditions during the Late Quaternary.

1.1. Ecology of Thalassiosira antarctica *Comber 1896*

Thalassiosira antarctica is an Antarctic diatom species rarely found living within sea ice (Hasle and Heimdal, 1968; Leventer and Dunbar, 1987; Fryxell and Kendrick, 1988; Zielinski and Gersonde, 1997), however, it is commonly described as a sea ice-associated diatom (i.e. living in waters with a high concentration of sea ice) linked with low sea surface temperature (SST) and low sea surface salinity (SSS) (Villareal and Fryxell, 1983). Blooms of *T. antarctica* are often recorded in waters associated with newly forming sea ice, such as the formation of platelet ice next to the Ross Sea ice

111 shelf (Cunningham and Leventer, 1998) and both frazil ice and platelet ice in the Weddell Sea
112 (Smetacek et al., 1992; Gleitz et al., 1998). In the Weddell Sea, it has also been recorded under
113 turbulent conditions (Gleitz et al., 1998) and from low salinity, nitrate-deplete, high pH crackpools
114 associated with summer melting ice (Gleitz et al., 1996). Although it is rare to find *T. antarctica* in
115 sea ice samples due to its requirement for open water to bloom (Bárcena et al., 1998) and its
116 sensitivity to low light intensities (Doucette and Fryxell, 1985; Fryxell et al., 1987), it has been
117 observed in some spring sea ice samples which suggests over-wintering in sea ice or re-suspension
118 from the sediments (Villareal and Fryxell, 1983).
119
120 *Thalassiosira antarctica* appears to be a summer and autumn bloom species. It has been observed
121 as a common component of the early summer phytoplankton around the Antarctic Peninsula
122 (Sommer, 1991) and was recorded in summer sediment traps in the Ross Sea (Leventer pers. comm.
123 in Taylor and McMinn, 2002). It has been described as a major component of phytoplankton
124 blooms in non-stratified or weakly stratified Antarctic surface waters (Cremer et al., 2003) (strong
125 water column stratification is usually associated with spring sea ice melt). *T. antarctica* has also
126 been associated with autumn bloom conditions in the Ross Sea with production of resting spores
127 related to the seasonally-late development of solid ice cover (Cunningham and Leventer, 1998).
128
129 However, contrary to these observations of natural populations, laboratory culture experiments
130 revealed that *T. antarctica* can grow well in reduced light conditions in temperatures as low as -4ºC
131 (Bartsch, 1989; Aletsee and Jahnke, 1992), and that vegetative *T. antarctica* cells can survive in sea
132 ice (Aletsee and Jahnke, 1992) and for prolonged periods of darkness (up to 214 days) without
133 forming resting spores (Peters and Thomas, 1996a). It is believed that the formation of
134 physiologically resting cells (identical in appearance to the vegetative cells) is induced by nutrient
135 stress (Peters and Thomas, 1996b), or by low light intensities beneath the summer diatom bloom
136 and/or associated nutrient depletion (Taylor and McMinn, 2001). However, culture experiments

carried out at -1.5ºC failed to induce resting spore formation by nitrogen depletion (Villareal and Fryxell, 1983). Significant lipid accumulation occurs in the resting spores as they form (Doucette and Fryxell, 1985) and this lipid synthesis has been attributed to a synergistic interaction between reduced light levels, reduced SST and increased SSS in other Antarctic sea-ice related phytoplankton species (Smith and Morris, 1980; Palmisano and Sullivan, 1982). In conclusion, the exact trigger for resting spore formation in *T. antarctica* is not well understood.

Observations of *T. antarctica* from the sediment record are almost exclusively the resting spore stage (Fryxell et al., 1981) (Figure 2). *T. antarctica* resting spores are heavily silicified and this has been suggested as a mechanism to facilitate rapid sinking out of freezing surface waters (Doucette and Fryxell, 1985). The heavily silicified resting spores are more readily transported, hence, often become concentrated in Antarctic near-coastal sediments (Gersonde and Wefer, 1987; Hemer and Harris, 2003). From spatially extensive surface sediment records, *T. antarctica* resting spores are most abundant beneath regions where February SSTs of 0 to 0.5ºC and where sea ice is present for at least 6 months per year with winter sea ice concentrations >70% and unconsolidated summer sea ice concentrations between 15-40% (Armand et al., 2005). Early Holocene sediments from Prydz Bay are characterised by abundant *T. antarctica* resting spores (average of 31% of the assemblage) and this has been related to seasonally warmer, more open marine conditions (Taylor and McMinn, 2002; Taylor and Leventer, 2003). In the Bransfield Strait, western Antarctic Peninsula, maximum abundance of *T. antarctica* resting spores in Holocene sediments is related to cold climate episodes (Bárcena et al., 1998), persistent influence of cold Weddell Sea water (Gersonde and Wefer, 1987; Leventer, 1991; Zielinski and Gersonde, 1997) and proximity to ice edge (Heroy et al., 2008). In deglacial and Holocene seasonally laminated Antarctic coastal sediments, *T. antarctica* resting spores commonly dominate the last recorded flux of the season, indicating their prior prevalence in mid- to late-summer blooms (as vegetative cells) and a relationship with falling temperatures (ice formation) and falling light levels (Maddison et al., 2005; Stickley et al., 2005).

163

164 *1.2. Ecology of* Porosira glacialis *(Grunow) Jörgensen 1905*

165

166 Generally, less is known about the ecological preferences of *Porosira glacialis* than for *T.*
167 *antarctica*. *Porosira glacialis* is a bipolar diatom species associated with cold coastal waters
168 adjacent to sea ice (Hasle, 1973; Taylor et al., 1997; Zielinski and Gersonde, 1997). Of the two
169 species of Antarctic *Porosira*, *P. pseudodenticulata* is commonly observed living in pack ice and
170 fast ice samples whereas *P. glacialis* is rarely recorded living in sea ice (Watanabe, 1988; Scott et
171 al., 1994; Armand, 1997). It has been suggested that *P. glacialis* predominantly grows in the open
172 ocean beyond the sea ice edge (Zielinski and Gersonde, 1997), however, *P. glacialis* has been
173 observed in waters with high concentrations of slush and wave-exposed shore ice although, again,
174 not living within the ice (Krebs et al., 1987). Similar to *T. antarctica*, in culture experiments, *P.*
175 *pseudodenticulata* survived prolonged periods of darkness (up to 272 days) by forming
176 physiologically resting cells, not by forming resting spores (Peters and Thomas, 1996a). Resting
177 spore formation was not induced at -1.5ºC (Villareal and Fryxell, 1983), and the exact mechanism
178 that promotes resting spore formation is not known.

179

180 *P. glacialis* is recorded in sediments predominantly as resting spores (Figure 2) and located
181 shoreward of the maximum winter sea ice extent (Armand, 1997). From the sediment record, *P.*
182 *glacialis* appears to grow in summer waters with SSTs ranging from -2 to 1.5ºC (slightly cooler
183 maximum temperature than *T. antarctica*) (Zielinski and Gersonde, 1997), and reaches maximum
184 abundances with February SSTs of 0 to 0.5ºC (Armand et al., 2005). From a spatially extensive
185 sediment surface data set, *P. glacialis* is most abundant beneath regions that experience at least 7.5
186 months per year sea ice cover (slightly longer than *T. antarctica*), with <30% summer sea ice
187 concentration and highly compacted winter sea ice (65-85% concentration) (Armand et al., 2005).
188 In deglacial, seasonally laminated sediments from Iceberg Alley, Mac.Roberston Shelf, *P. glacialis*

RS are abundant in *Thalassiosira antarctica* RS sub-laminae that record the final flux event of the year, thus suggesting a similarity in their growth requirements (Stickley et al., 2005). In Holocene laminated sediments from the Mertz-Ninnis Trough, George V Coast, *P. glacialis* RS sub-laminae are interpreted as representing late summer/autumn deposition as sea ice concentration in the Mertz Glacier polynya increased (Maddison et al., 2006).

2. Materials and Methods

2.1. Materials

This study uses a suite of Late Quaternary sediment cores recovered from the East Antarctic margin. Cores from Mertz Ninnis Trough (NBP0101 JPC10/KC10A), Iceberg Alley (NBP0101 JPC43B) and Svenner Channel (NBP0101 JPC24) were recovered during RVIB *Nathaniel B. Palmer* cruise NBP0101 during 2001 (Table 1, Figure 1). Cores from the Dumont d'Urville Trough (MD03-2597/MD03-2601) were recovered during the MD130-Images X-CADO cruise of RV *Marion Dufresne II* in 2003 (Table 1, Figure 1). All cores are, in part, seasonally laminated with the remaining stratigraphy being either intermittently laminated or homogenous siliceous-mud ooze (Crosta et al., 2005; Leventer et al., 2006; Maddison, 2006; Maddison et al., 2006). Intervals selected for lamina-scale analyses and down-core diatom assemblage analysis in this study are illustrated in Figure 1 and listed in Table 1.

The early Holocene and Neoglacial (Figure 1) laminated sediment sequences from Mertz Ninnis Trough were deposited approximately 30 km from the coast, beneath the site of a persistent winter polynya (Maddison et al., 2006). The two cores from Dumont d'Urville Trough were recovered from biogenic drift deposits that accumulated in small depressions, approximately 30 km and 60 km

offshore, within the trough (Crosta et al., 2005). The Dumont d'Urville Trough region is an open coastline with a typical regime of advance and retreat of seasonal sea ice, with the episodic presence of a polynya (Arrigo and Van Dijken, 2003). Today, the sites are covered by sea ice for 8-9 months of the year (Schweitzer, 1995). During the deposition of the deglacial laminated sediments in Iceberg Alley the long, across-shelf trough that comprises the basin was surrounded by a calving bay re-entrant (Leventer et al., 2006). This meant that even though the site is approximately 70 km offshore today, it would have been subject to a seasonal sea ice retreat and advance regime typical of more coastal sites. Svenner Channel is a coast-parallel trough on the eastern margin of Prydz Bay. The core site is approximately 60 km from the coast and is subject to a typical seasonal sea ice advance and retreat regime that results in a yearly sea ice presence of 10 months.

2.2. Lamina analyses: BSEI and LM sediment fabric analysis and quantitative diatom assemblage analysis

Laminated sediments (Figure 1) were embedded in resin and polished thin sections were produced for microscope analysis following the methods outlined in Maddison et al. (2006, NBP0101 JPC10/KC10A, MD03-2597), Denis et al. (2006, MD03-2601) and Stickley et al. (2005, NBP0101 JPC43B). Laminated sequences (polished thin sections) were logged for sediment fabric and diatom assemblages at the 100 micron-scale using either scanning electron microscopy backscattered electron imagery (BSEI, Pike and Kemp, 1996; Pearce et al., 1998) or optical light microscopy (LM, Denis et al., 2006) (Table 2). For core sites NBP0101 JPC10/KC10A and MD03-2597 additional quantitative diatom assemblage analyses were carried on specific lamination types following the method outlined in Maddison et al. (2006). These additional analyses facilitated quantitative comparison of the relative abundance of *T. antarctica* RS and *P. glacialis* RS in the laminations, as opposed to the more qualitative techniques involved in thin section analysis using BSEI and LM. Data are presented as absolute abundance (valves per gramme), relative abundance

and *Hyalochaete Chaetoceros* resting spore-free (CRS-free) relative abundance (Table 3). CRS-free abundance is commonly used in Antarctic diatom assemblage analysis when CRS overwhelmingly dominate every assemblage (Leventer et al., 1996; Allen et al., 2005). The CRS-free abundance allows the ecological information within the minor species assemblage to be critically examined.

2.3. Down-core quantitative diatom assemblage analysis

Down-core quantitative diatom assemblage analysis was carried out on MD03-2601 (Dumont d'Urville Trough) and NBP0101 JPC24 (Svenner Channel) following the methods outlined in Crosta et al. (2007). These records allow the relationship between *T. antarctica* RS and *P. glacialis* RS, deduced from lamination-scale analyses of mainly deglacial sediments, to be investigated over the duration of the Holocene. *Porosira glacialis* RS and *P. pseudodenticulata* RS are grouped together, however, *P. glacialis* RS overwhelmingly dominates the group. *P. pseudodenticulata* has no distinct central annulus, a slightly larger diameter and fewer areolae in 10 µm (~60-80 µm; 10-12) than *P. glacilalis* (30-40 µm; 25-26) which often has a distinct central annulus. The two forms of *T. antarctica* RS are grouped (T1 and T2, Buffen et al., 2007), however, the cool *T. antarctica* RS form (T1) overwhelmingly dominates in both Dumont d'Urville Trough and Svenner Channel sediments.

2.4. Modelled Holocene surface temperatures and sea ice concentrations

The diatom abundance and sediment fabric data and interpretations will be compared with the results of a 9000-yr Holocene climate simulation using the ECBilt-CLIO-VECODE coupled atmosphere-sea ice-ocean-vegetation model forced with annually varying orbital parameters (monthly insolation at 60°S) and atmospheric greenhouse gas (carbon dioxide and methane)

concentrations derived from ice cores (Opsteegh et al., 1998; Goosse and Fichefet, 1999; Brovkin et al., 2002; Renssen et al., 2005). In the model, the vernal equinox is fixed at day 81 and the year is divided into 12 months of 30 days. All other forcings (e.g. solar constant, other greenhouse gases, ice sheet configuration) are set at AD 1750 values, hence, changes in ice sheet volume are not taken into account in the simulation used here. As well as comparing with the published East Antarctic modelled summer temperature record of Renssen et al. (2005), we will also compare our results to a sub-set of the whole model output for the Adélie Land sector that encompasses the Dumont d'Urville Trough core sites (south of 60°S, 140°E-150°E). Two 1000-year time periods from the Adélie Land mean monthly surface temperature and sea ice concentrations were selected to provide a measure of typical mean monthly conditions; the interval 4999-4000 yr BP was selected as typical of the Hypsithermal and 1999-1000 yr BP selected as representative of the Neoglacial. These two time periods were compared to investigate statistically significant differences in modelled monthly parameters between the Hypsithermal and Neoglacial. Significant differences in the means were found using a standard z-test (with 2-tailed critical values) for assessing differences in the means between large sample sets (Table 4).

3. Results

3.1 Laminated sediments – BSEI, LM and quantitative diatom assemblage analysis

Data for the lamina-scale diatom assemblage analyses, using BSEI, LM and quantitative abundance, come from both published sources and from new analyses. BSEI lamina characterisations for sediments from the Mertz-Ninnis Trough (NBP0101 JPC10/KC10A) are summarised from Maddison (2006) and Maddison et al. (2006). Similar data for the Dumont d'Urville Trough (MD03-2597) are summarised from Maddison (2006) and LM lamina data (MD03-2601) are summarised from Denis et al. (2006). Lamina-scale diatom assemblage data for sediments from

Iceberg Alley (NBP0101 JPC43B) are a combination of both published (Stickley et al., 2005, interval 21.84-23.96 m) and previously unpublished data (Stickley and Pike: interval 19.30-21.84 m). Tables 2 and 3 provide a summary of these data containing only the lamina or sub-lamina data relevant to this study.

3.1.1. *Thalassiosira antarctica* RS sub-laminae

Analysis of lamina occurrence data from the spectacularly laminated deglacial sediments of the East Antarctic margin reveals that when sub-laminae characterised by *T. antarctica* RS or *P. glacialis* RS occur, usually: (1) either one or the other species is dominant; and (2) they are found in a similar position within the seasonal succession of diatom assemblages and lamina types, i.e. at the end of the season of diatom production and subsequent flux to the sediment, late summer or autumn (Stickley et al., 2005; Denis et al., 2006; Maddison, 2006). In deglacial Iceberg Alley sediment, 43 of 68 *T. antarctica* RS sub-laminae occur in this position above a summer lamina (Table 2) and, consequently, directly below the following spring diatom ooze lamina from which they are separated by a sharp contact delineating the winter hiatus. Further, when a summer lamination is not present, 25 of 68 occurrences of *T. antarctica* RS sub-laminae follow a transitional lamination (Table 2), defined as having some characteristics of both spring diatom ooze laminae and summer terrigenous-rich laminae (Stickley et al., 2005). These transitional laminae nearly always grade upwards from a spring diatom ooze lamina and usually grade into a summer terrigenous-rich lamina, however, sometimes these transitional laminae are abruptly overlain by the following spring diatom ooze laminae. Usually, it is at the top of these latter transitional laminae that *T. antarctica* RS sub-laminae occur. When *T. antarctica* RS sub-laminae occur within the annual sediment increment, the mean annual sediment thickness is 2% greater than if sub-laminae do not occur. Further, if a summer lamination is followed by a *T. antarctica* RS sub-lamina, the summer lamina is, on average, 7% thicker than one that is not associated with a sub-lamina (Table 2). Qualitative

318 analysis of *T. antarctica* RS sub-laminae from Iceberg Alley also reveals that *P. glacialis* RS are
319 more abundant in the sub-laminae than in the summer, terrigenous-rich laminae.
320
321 LM analysis of lamina sequences from the Holocene sediments of the less coastal MD03-2601 core
322 from Dumont d'Urville Trough shows the presence of sub-laminae of *T. antarctica* RS associated
323 with late summer/autumn in Hypsithermal-age sediments and the absence of the sub-laminae in
324 Neoglacial-age sediments (Table 2, Denis et al., 2006). During the Hypsithermal period, annual
325 sediment thickness was 46 mm compared with 21 mm during the Neoglacial, and mean thickness of
326 *T. antarctica* RS sub-laminae during the Hypsithermal was 0.371 mm (Table 2, Denis et al., 2006).
327 In contrast to the other, more coastal core site from Dumont d'Urville Trough (MD03-2597) these
328 sections from MD03-2601 do not contain any *P. glacialis* RS sub-laminae during the Neoglacial.
329
330 3.1.2 *Porosira glacialis* RS sub-laminae
331 Nineteen out of twenty two occurrences of *P. glacialis* RS sub-laminae in deglacial Mertz-Ninnis
332 Trough sediment appear in a late summer/autumn position in the seasonal lamina succession (Table
333 2). Quantitative diatom abundance analysis of Mertz-Ninnis Trough laminations reveals that
334 although, in absolute terms, *P. glacialis* RS have a similar abundance in summer mixed diatom
335 laminae as they do in *P. glacialis* RS sub-laminae (Table 3, Maddison et al., 2006), *P. glacialis* RS
336 comprise, on average, 11.35% of the CRS-free assemblage in *P. glacialis* RS sub-laminae and only
337 2.29% in the summer mixed assemblage laminae (Table 3, Maddison et al., 2006). At this site, *T.*
338 *antarctica* RS are absent from both the summer mixed diatom laminae and the *P. glacialis* RS sub-
339 laminae (Table 3, Maddison et al., 2006). When a *P. glacialis* sub-lamina occurs within the annual
340 sediment increment, the mean annual sediment thickness is 18% greater than if a sub-lamina does
341 not occur (Table 2). BSEI analysis of a 0.28 m-long (17 year) sequence of early Neoglacial-age
342 laminations from this site (NBP0101 KC10A; Table 1 and Figure 1) does not reveal any *T.*
343 *antarctica* RS or *P. glacialis* RS sub-laminae (Maddison, 2006).

In Neoglacial laminated sediments from the more coastal Dumont d'Urville Trough core (MD03-2597), in 23 out of 26 years when *P. glacialis* RS sub-laminae occur, the sub-laminae appear in a late summer/autumn position (Table 2, Maddison, 2006), separated with a sharp contact from the overlying spring lamination. Quantitative diatom abundance analysis reveals that, in absolute terms, *P. glacialis* RS are more than 2.5 times as abundant in *P. glacialis* RS sub-laminae than they are in terrigenous-rich, summer mixed assemblage laminae. Further, *T. antarctica* RS are more than 2.5 times as abundant in *P. glacialis* RS sub-laminae than in terrigenous-rich, summer mixed assemblage laminae (Table 3, Maddison, 2006). When *P. glacialis* RS sub-laminae occur within the annual sediment increment, the mean annual sediment thickness is 12% greater than if sub-laminae do not occur (Table 2).

3.2. Holocene records from Dumont d'Urville Trough and Svenner Channel

Holocene relative abundance of *T. antarctica* RS and *P. glacialis* RS from Dumont d'Urville Trough (MD03-2601) and Svenner Channel (NBP0101 JPC24) (Figure 1) are shown in Figure 3. In general, at both sites, relative abundances of *T. antarctica* RS are higher than *P. glacialis* RS. In the Dumont d'Urville Trough, the relative abundance of *T. antarctica* RS steadily rises to a peak at ~8.9 cal kyr BP (Figure 3B). Abundance then generally stays above 10% until ~3.4 cal kyr BP when it falls below 10% until ~2 cal kyr BP. Abundance then becomes very low (<5%) between 2 cal kyr BP until ~1.1 cal kyr BP, after which it recovers to about 10% at the top of the core. Relative abundance of *P. glacialis* RS displays an approximately inverse pattern. Abundance remains above 2% from ~10.8 cal kyr BP until ~8.7 cal kyr BP (Figure 3C), with a slight dip in abundance around 9.8 cal kyr BP. At 8.7 cal kyr BP, abundance falls abruptly below 2% until ~3.4 cal kyr BP, when it abruptly rises to above 2% until ~2.8 cal kyr BP when it falls below, and stays

369 below, 2% until ~2 cal kyr BP. After 2.0 cal kyr BP, abundance rises to above 2% and then steadily
370 falls towards the top of the core (~1 cal kyr BP).
371
372 In Svenner Channel, *T. antarctica* RS relative abundance rises from 11.2 cal kyr BP to a peak of
373 >20% around 9.8 cal kyr BP (Figure 3E). Abundance dips below 20% around 9 cal kyr BP, rises to
374 above 20% at ~8.7 cal kyr BP and then increases steadily to a peak at ~4.4 cal kyr BP. Relative
375 abundance begins to decline and falls below 20% at ~3.4 cal kyr BP; it remains below 20% until the
376 top of the core (~0.67 cal kyr BP). The relative abundance of *P. glacialis* RS remains below ~2%
377 from 11.2 cal kyr BP until ~8.7 cal kyr BP when it begins to steadily rise (Figure 3F). At ~4.3 cal
378 kyr BP, abundance rises above 2% and stays high until ~1 cal kyr BP when it falls below 2 % at the
379 top of the core.
380
381 The relationship between *T. antarctica* RS and *P. glacialis* RS can be further investigated by
382 looking at the ratio between the two diatoms, and also the statistical correlation between the two
383 species curves. The ratio between *P. glacialis* RS and *T. antarctica* RS (i.e. relative abundance of
384 *P. glacialis* RS/relative abundance of *T. antarctica* RS) in Dumont d'Urville Trough is approaching
385 0.5 from the base of the core (~10.8 cal kyr BP) until ~10 cal kyr BP where it abruptly falls to very
386 low values (Figure 3D). The ratio remains very low until ~3.4 cal kyr BP when it abruptly rises to
387 >0.1 up to the top of the core (~1 cal kyr BP). Between ~2.8 cal kyr BP and ~2 cal kyr BP, the ratio
388 falls, however, generally remains above 0.1. In Svenner Channel, the ratio between *P. glacialis* RS
389 and *T. antarctica* RS remains generally <0.1 from ~11.2 cal kyr BP until ~4.3 cal kyr BP when it
390 begins to rise (Figure 3G). The ratio reaches peak values (~0.5) at ~2.8 cal kyr BP and generally
391 remains above 0.2 up to the top of the core (~0.7 cal kyr BP). The Pearson correlation coefficient
392 (r) between the relative abundance of *T. antarctica* RS and *P. glacialis* RS is -0.19 for the Dumont
393 d'Urville record (n=528). This correlation coefficient appears weak, but a test of significance of r
394 demonstrates that threshold for significant values of r for sample sizes of n=528, at the 99%

significance level, is 0.14 (Lowry, 2008). There is no significant correlation between the relative abundances of *T. antarctica* RS and *P. glacialis* RS in the Svenner Channel record. The correlation coefficient is negative, but not significant (r=-0.0004; n=348). However, the significant negative correlation between *T. antarctica* RS and *P. glacialis* RS for Dumont d'Urville Trough supports the qualitative observations of an inverse relationship between the two taxa.

The diatom relative abundance curves are also compared with the modelled mean October to April (i.e. austral summer) surface temperature record for the Holocene of East Antarctica (Renssen et al., 2005) (Figure 3A). The modelled surface temperature record reveals temperatures warming from ~0.4°C warmer than pre-industrial levels at 9.0 kyr BP, to temperatures ~1.0°C warmer than pre-industrial levels at ~4.3 kyr BP. Modelled temperatures then decline steadily until the end of the record, approximately 300 yr BP. The Pearson correlation between the relative abundance of *T. antarctica* RS and modelled mean summer temperature in Dumont d'Urville Trough and Svenner Channel is 0.44 and 0.64, respectively. The Pearson correlation between the relative abundance of *P. glacialis* RS and modelled mean summer temperature in Dumont d'Urville Trough and Svenner Channel is -0.48 and -0.11, respectively. The Pearson correlation between the modelled mean summer temperature and the ratio *P. glacialis* RS:*T. antarctica* RS is -0.55 for Dumont d'Urville Trough and -0.40 for Svenner Channel. All but one of these correlation coefficient values are above the threshold values of the Pearson's test of significance (r=-0.11 falls below the threshold). This highlights a positive correlation between the relative abundance of *T. antarctica* RS and modelled mean summer temperature; a negative correlation between relative abundance of *P. glacialis* RS and modelled mean summer temperature; and a more robust negative correlation between the ratio *P. glacialis* RS:*T. antarctica* RS and modelled mean summer temperature.

4. Interpretation and Discussion

4.1. Mechanism for formation of T. antarctica *and* P. glacialis *resting spore sub-laminae*

When sub-laminae characterised by *T. antarctica* RS or *P. glacialis* RS occur in the laminated sediments from the East Antarctic margin, three features are consistent: (1) one or the other species is dominant; (2) the sub-laminae predominantly occur in the same position within the seasonal sedimentary sequence – late summer to autumn; and (3) overall annual sediment thickness is greater when sub-laminae are present (in deglacial Iceberg Alley sediments, the sub-laminae are also associated with summer laminations that are thicker than average indicating increased summer production and flux to the sediments). Hence (2) and (3) can be interpreted together as indicating that the sub-laminae are associated with years of higher diatom flux to the sediment. The occurrence of *T. antarctica* RS and *P. glacialis* RS sub-laminae (and thicker summer laminations) could indicate either a longer duration summer season of diatom productivity, promoting greater overall flux to the sediment, or enhanced summer conditions that favour higher *T. antarctica* and *P. glacialis* vegetative production, hence production and flux of the resting spores to the sediment in autumn.

Thalassiosira antarctica RS and *P. glacialis* RS sub-lamina production is likely to be related to a slow break up of sea ice over a sustained period in spring, i.e. a slow increase of temperatures over a few weeks so that when light levels increase sufficiently to promote vegetative cell growth there is a relatively high sea ice concentration that significantly effects surface water properties. *Porosira glacialis* and *T. antarctica* have both been found associated with spring sea ice-rich regions (Villareal and Fryxell, 1983; Krebs et al., 1987). Relatively high spring sea ice concentrations would lead to summer production favouring sea ice-associated diatoms such as *T. antarctica* and *P. glacialis* (standing stocks enhanced by ‘icy’ spring) and both species are known to be abundant in Antarctic summer waters (Sommer, 1991; Zielinski and Gersonde, 1997; Cremer et al., 2003). Finally, sea ice formation in the autumn, accompanied by lowering SSTs, increased salinity and

447 lowering light levels (Doucette and Fryxell, 1985; Fryxell et al., 1987; Cunningham and Leventer,
448 1998), would induce resting spore formation from a vegetative population that was sufficiently
449 large to produce a sub-lamina in the sediments (Stickley et al., 2005; Denis et al., 2006; Maddison
450 et al., 2006). Years without sub-laminae suggest more rapid melting and break-up of sea ice in
451 spring favouring more marginal ice zone/open water species and reduced growth of *T. antarctica*
452 and *P. glacialis* in the subsequent summer. Lower summer vegetative populations of *T. antarctica*
453 and *P. glacialis* would not lead to the production of sufficient numbers of resting spores to produce
454 a sub-lamina in autumn.
455
456 Key to confirming this sea ice-based model of sub-lamina formation are the two cores from Dumont
457 d'Urville Trough which are geographically close to each other and would have experienced similar
458 changes in external forcing (i.e. by insolation and greenhouse gases). At MD03-2601, during the
459 Hypsithermal, *T. antarctica* RS sub-laminae were preserved (core MD03-2597 did not recover
460 Hypsithermal-age sediments). In the Neoglacial, no sub-laminae of either species were preserved at
461 site MD03-2601, although higher relative abundances of *P. glacialis* RS are observed (Figure 3C),
462 whereas *P. glacialis* RS sub-laminae were preserved at MD03-2597 (Table 2). In the modern day,
463 site MD03-2597 is covered by less than 65% sea ice concentration for, on average, 111 days of the
464 year, whereas site MD03-2601 is subject to less than 65% sea ice concentration for only 94 days of
465 the year (difference between means is significant at >95%; mean values extracted from satellite-
466 derived daily sea ice concentrations for 26 years between 1979 and 2006, National Snow and Ice
467 Data Centre, http://nsidc.org/data/nsidc-0079.html). Site MD03-2597 becomes 'ice-free'
468 (consistently less than 65% sea ice concentration), on average, 19 days earlier in the spring than site
469 MD03-2061 because the ice-edge not only retreats parallel with the coastline, but also retreats in a
470 westward direction along the coast towards the Dumont d'Urville Trough. This is due to the areal
471 expansion of the coastal Mertz Glacier Polynya, which merges with the open ocean in summer. So,
472 not only are there less ice-free days at MD03-2601, the sea ice retreats later in the spring. The

473 combined evidence of higher relative abundance of *P. glacialis* RS (MD03-2601) and the presence
474 of P. glacialis RS sub-laminae (MD03-2597) in Neoglacial sediments, along with the cessation of T.
475 antarctica RS sub-laminae formation (MD03-2601), suggests that increasingly higher winter and
476 spring sea ice concentrations occurred in the Dumont d'Urville Trough region in the Neoglacial,
477 relative to the Hypsithermal period. Perhaps the environment became either too icy (given modern
478 seasonal sea ice differences detailed above) or, more likely, had too short an ice-free summer
479 season at site MD03-2601 during the Neoglacial for even *P. glacialis* to be able to form large
480 enough populations to promote significant flux of resting spores to the sea floor and subsequent
481 sub-laminae formation.
482
483 *4.2. Environmental controls on the* P. glacialis *RS:*T. antarctica *RS ratio in Holocene sediments*
484
485 From the lamination data, *T. antarctica* RS and *P. glacialis* RS sub-laminae are both interpreted as
486 representing years with relatively high spring sea ice concentrations, however, what threshold under
487 these conditions would govern changes in the relative abundance of the two species seen throughout
488 the Holocene (Figure 3), given that they appear to have similar ecologies? Here we combine our
489 sea ice-based mechanism of sub-lamina formation with published ecological preferences and
490 modelled Holocene surface temperature and sea ice concentrations from the Adélie Land sector
491 (Table 4, Figure 4) to present a model of the environmental conditions that alter the relative
492 abundance of *T. antarctica* RS and *P. glacialis* RS in the sediments.
493
494 *P. glacialis* appears to prefer somewhat higher winter and spring sea ice concentrations than *T.*
495 *antarctica.* Maximum abundances of *P. glacialis* RS in the sediment are found beneath regions
496 subject to >7.5 months per year sea ice cover (*T. antarctica* prefers >6 months), <30% summer sea
497 ice concentration (*T. antarctica* similar) and highly compacted winter sea ice (up to 85%
498 concentration; *T. antarctica* prefers slightly less, but still >70%) (Armand et al., 2005). These

ecological observations are supported by our Holocene records and comparisons with the modelled summer surface temperatures from East Antarctica (Renssen et al., 2005). Increased abundance of *T. antarctica* RS in the sediments from Dumont d'Urville Trough and Svenner Channel is positively correlated with modelled summer surface temperatures whereas increased abundance of *P. glacialis* RS is negatively correlated with modelled summer surface temperatures (Figure 3).

The modelled sea ice concentration and surface temperature records for the Adélie Land sector suggest that the cool Neoglacial period had higher winter and early spring sea ice concentrations than the mid Holocene Hypsithermal (Table 4, Figure 4), with significantly lower late spring and early summer temperatures. In autumn, the Neoglacial had lower sea ice concentrations than the Hypsithermal with slightly higher temperatures. This model output supports the interpretation from ecological and seasonal sedimentological data that *P. glacialis* prefers slightly cooler and 'icier' winter and spring conditions than *T. antarctica*, which is why its abundance was enhanced during the Neoglacial off both Adélie Land and Princess Elizabeth Land. A subsequent long summer/autumn season, as suggested by the model data, would favour the build-up of larger populations of *P. glacialis* and concomitantly reduced populations of *T. antarctica*. Our interpretations are in agreement with those of Crosta et al. (2008) who state that seasonal sea ice distribution during the Holocene of East Antarctica is more complicated than a simple pattern of less sea ice during the warmer Hypsithermal, and more during the cooler Neoglacial.

4.3. P. glacialis *RS:*T. antarctica *RS – a new sediment proxy for winter and spring sea ice concentrations*

The results from Dumont d'Urville Trough (MD03-2601) and Svenner Channel sediments presented here indicate that 0.1 appears to be a significant threshold value for the ratio *P. glacialis* RS:*T. antarctica* RS. An increase above 0.1 accompanies an important environmental change to

525 increased winter sea ice concentration, cooler spring seasons with increased sea ice, and slightly
526 warmer autumn seasons with less sea ice. In the Holocene sediments of coastal East Antarctica, the
527 ratio changes from <0.1 to >0.1 between 4.3-3.4 cal kyr BP (i.e the transition from warmer
528 Hypsithermal conditions to cooler, Neoglacial conditions, Masson et al., 2000; Crosta et al., 2007).
529 However, it is possible to use the ecological information in an attempt to be more quantitative than
530 this. Using the ecological preferences of *P. glacialis* and *T. antarctica* and it's distribution in
531 modern core top samples (Armand et al., 2005), an increase in the sediment ratio above 0.1 (i.e.
532 enhanced *P. glacialis* RS and/or relatively reduced *T. antarctica* RS abundance) appears to indicate
533 a change from ~7.5 months of annual sea ice cover (favouring *T. antarctica* production), to much
534 greater than 7.5 months of annual sea ice cover (enhancing *P. glacialis* production), and an increase
535 from ~70% winter sea ice concentration (favouring subsequent *T. antarctica* production) to highly
536 compacted winter sea ice above 80% concentration (enhancing *P. glacialis* production). Although
537 these may not seem like large changes, they appear to be key manifestations of the changes between
538 warmer and cooler Holocene climate states as reflected in the diatom fossil record, and are in line
539 with the changes suggested by previous diatom evidence for the Hypsithermal-Neoglacial transition
540 (Crosta et al., 2008).
541
542 Attempts to apply the *P. glacialis* RS:*T. antarctica* RS proxy to west Antarctic Peninsula (WAP)
543 diatom records from Palmer Deep (Taylor and Sjunneskog, 2002) and Bransfield Strait (Heroy et
544 al., 2008) have met with limited success because the relative warmth of the WAP compared to the
545 East Antarctica margin limits the abundance of *P. glacialis* RS in the sediments to be almost always
546 less than 10% of *T. antarctica* RS. However, a preliminary analysis of Holocene diatom abundance
547 records from the cooler NW Weddell Sea has proved promising in that stratigraphic intervals when
548 *P. glacialis* RS:*T. antarctica* RS was >0.1 (interpreted as representing cool, sea ice-rich winter and
549 spring conditions) are also intervals of high abundance of other sea ice-related diatoms such as
550 *Fragilariopsis curta, F. cylindrus* and *Thalassiosira tumida* (Anna Hey, personal communication,

2008). This demonstrates the potential wider applicability of the *P. glacialis* RS:*T. antarctica* RS ratio around the Antarctic coast.

5. Conclusions

This synthesis of information on the abundance of *Thalassiosira antarctica* and *Porosira glacialis* has shown that these two diatoms have similar ecological preferences. The combination of modern phytoplankton analyses, laboratory experiments and late Quaternary laminated sediment records reveals that high fluxes of *T. antarctica* RS and *P. glacialis* RS to the sediment are associated with prior high winter and spring sea ice concentrations that promote the build-up of large vegetative cell populations. In late autumn, abrupt sea ice advance, accompanied by decreasing temperatures and irradiance and increased salinities promotes resting spore formation from high summer/autumn standing stocks. The investigation of two core records from the Dumont d'Urville Trough and one from Svenner Channel showed that despite their similar ecological preferences, there were interesting differences in the Holocene occurrence of the two taxa. Relative abundance of *T. antarctica* RS peaked during the warm mid-Holocene Hypsithermal period and declined into the cooler Neoglacial, whereas relative abundance of *P. glacialis* RS peaked during the late Holocene, cool Neoglacial period. Increased *P. glacialis* RS abundance appeared to be linked with higher winter and spring sea ice concentrations than *T. antarctica* RS. These conclusions are corroborated by a comparison with modelled Holocene sea ice concentrations and surface temperatures for the Adélie Land sector. The model output reveals higher winter and early spring sea ice concentrations, and lower spring and early summer temperatures during the Neoglacial relative to the Hypsithermal (which would promote increased populations of *P. glacialis*). Investigation of the ratio of relative abundance of the two diatoms, *P. glacialis* RS:*T. antarctica* RS, revealed that a threshold of 0.1 was important. The ratio abruptly increased from <0.1 to >0.1 at the Hypsithermal to Neoglacial transition. An increase in the ratio *P. glacialis* RS:*T. antarctica* RS to greater than 0.1 appears to

indicate a change from ~7.5 months of annual sea ice cover to much greater than 7.5 months of cover, and an increase of winter sea ice concentrations from 70% to >80%. An attempt to apply the *P. glacialis* RS:*T. antarctica* RS ratio to other core sites from West Antarctica, in particular the NW Weddell Sea, shows that the relationship between these two diatom species may be able to reveal information about past winter and spring sea ice concentrations around the Antarctic margin.

Acknowledgements

This research was funded by Natural Environment Research Council (NERC) research grant NER/A/S/2001/01106 (JP), NERC postgraduate research studentship NER/A/2002/10350 (EJM at the School of Earth and Ocean Sciences, Cardiff University). XC was funded by the project TARDHOL through the national EVE-LEFE program (INSU-CNRS). This manuscript was developed during JP's stay at EPOC, funded by the Invited Professor Scheme of Bordeaux I University. The climate modelling work was supported by the Netherlands Organization for Scientific Research (HR). JP would like to thank Captain Joe Borkowski, the Edison Chouest Offshore crew, the Raytheon Polar Services Company staff and scientific party aboard the RVIB *Nathaniel B. Palmer* during cruise NBP01-01, and the staff at the Antarctic Research Facility (Florida State University) for assistance with sampling. We (JP, CES, EJM, XC) particularly acknowledge discussion and encouragement over many stages of this research by Amy Leventer. XC personally thanks members of the Images X (CADO) cruise and from cruise NBP01-01 for providing data and suggestions. Logistical support for Images X (CADO) cruise was provided by IPEV-TAAF. JP would also like to thank Charlotte Sjunneskog for sharing west Antarctic Peninsula diatom data sets, and Ian Thomas for assistance in handling the NSIDC satellite daily sea ice concentration data set. Finally we would like to thank María Ángeles Bárcena Pernía and one anonymous reviewer for their careful consideration of our manuscript.

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604

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762 **Table and Figure Captions**

763

764 Table 1: East Antarctica margin sediment core information, including details of location, length,
765 distance from coast, core intervals analysed and age of intervals analysed.

766

767 Table 2: Summary of lamina and sub-lamina thickness measurements from BSEI and LM of East
768 Antarctic laminated sediment sequences.

769

770 Table 3: Quantitative abundance of *Porosira glacialis* RS and *Thalassiosira antarctica* RS from
771 selected East Antarctic sediment laminae and sub-laminae.

772

773 Table 4: Summary of Adélie Land sector modelled Holocene surface temperature and sea ice
774 concentrations for typical Hypsithermal (4000-4999 yr BP) and typical Neoglacial (1000-1999 yr
775 BP) periods (extracted from Renssen et al., 2005). Surface temperatures and sea ice concentrations
776 are given as anomalies from the pre-industrial mean (1000-250 yr BP).

777

778 Figure 1: Locations of the East Antarctic margin sediment cores used in this investigation. AL =
779 Adélie Land and PEL = Princess Elizabeth Land. The intervals sampled from each of the cores are
780 shown by the black (BSEI and LM sediment fabric analyses) and grey (Holocene down-core
781 quantitative diatom abundance analyses). The presence of *Thalassiosira antarctica* RS sub-laminae
782 is indicated by white and *Porosira glacialis* RS sub-laminae by a vertical line.

783

784 Figure 2: Light microscope (LM) and scanning electron microscope (SEM) images of
785 *Thalassiosira antarctica* and *Porosira glacialis* resting spores. SEM micrographs taken of Au-Pd
786 coated, lamina parallel sediment fracture surfaces. A**-B.** LM micrographs of *T. antarctica* resting
787 spores (NBP01-01 JPC10, 19.536 cm). **C-D.** Secondary electron SEM micrographs of *T.*

788 *antarctica* resting spores (MD03-2597, 5307.5 cm, scale bars G = 5 microns, H = 10 microns). **E-**
789 **F.** LM micrographs of *P. glacialis* resting spores (NBP01-01 JPC10, 19.536 cm). **G-H.** Secondary
790 electron SEM micrographs of *P. glacialis* resting spores (NBP01-01 JPC10, 19.463 cm; scale bars
791 C = 10 microns, D = 50 microns).
792
793 Figure 3: Holocene *Thalassiosira antarctica* and *Porosira glacialis* resting spore abundance from
794 Dumont d'Urville Trough (MD03-2601) and Svenner Channel (NBP01-01 JPC24). **A.** Modelled
795 mean summer (October to April) surface temperature (relative to the pre-industrial mean (1000-250
796 yr BP)) from Renssen et al. (2005). **B-D.** Dumont d'Urville Trough records. **B.** Relative
797 abundance of *T. antarctica* RS. **C.** Relative abundance of *P. glacialis* RS. **D.** Ratio of *P. glacialis*
798 RS:*T. antarctica* RS. **E-G.** Svenner Channel records. **E.** Relative abundance of *T. antarctica* RS.
799 **F.** Relative abundance of *P. glacialis* RS. **G.** Ratio of *P. glacialis* RS:*T. antarctica* RS.
800 Neoglacial and Hypsithermal intervals are defined following Crosta et al. (2005).
801
802 Figure 4: Schematic diagram illustrating differences modelled sea ice concentrations and surface
803 temperatures between Hypsithermal and Neoglacial. Differences significant at the 99% confidence
804 interval are shown with horizontal lines and differences at the 95% confidence interval are shown
805 with horizontal curves. Where the Hypsithermal and Neoglacial lines overlap there is no
806 statistically significant difference between the two records.
807
808

Table 1

Cruise	Location	Core	Latitude	Longitude	Water depth / m	Distance from coast / km	Core length/ m	Interval(s) analysed / m	Age /cal yr BP[1]
NBP01-01	Mertz-Ninnis Trough	JPC10 KC10A	66º34.334′S	143º05.168′E	850	~30	21.35 2.50	Thin sections: 17.36-20.60 2.05-2.38	6756-11384 3820-3892
MD130-Images X-CADO	Dumont d'Urville Trough	MD03-2597	66º24.74′S	140º25.26′E	1025	~30	57.34	Thin sections: 13 x 15-cm-intervals between 18.75-56.83	925-2814
MD130-Images X-CADO	Dumont d'Urville Trough	MD03-2601	66º03.07′S	138º33.43′E	746	~60	40.24	Diatom abundance: 0-40.25 Thin sections: 6.19-6.485 & 18.808-19.107	1000-10843 ~2550 ~5635
NBP01-01	Iceberg Alley	JPC43B	66º55.943′S	64º07.376′E	465	~75	23.96	Thin sections: 19.30-23.96	10500-11500
NBP01-01	Svenner Channel	JPC24	68º41.660′S	76º42.557′E	848	~60	15.35	Diatom abundance: 0-17.00	655-11082

[1] Age models from Denis et al. (2006), Maddison (2006), Maddison et al. (2006), and Leventer et al. (2006)

Table 2

Location	*P. glacialis* RS or *T. antarctica* RS	Sediment Increment Type	Mean Thickness (standard deviation) /mm	No. of Measure-ments (n)	Minimum thickness /mm	Maximum thickness /mm
Mertz-Ninnis Trough (NBP0101 JPC10) Early Holocene	*P. glacialis* RS	Annual thickness	17.5 (16.9)	116	1.8	103.2
		Annual thickness if *P. glacialis* RS sub-laminae are present	20.6 (14.6)	22	3.0	53.3
		P. glacialis RS sub-lamina thickness	1.4 (1.1)	22	0.5	5.5
Dumont d'Urville Trough (MD03-2597) Neoglacial	*P. glacialis* RS	Annual thickness	18.1 (9.6)	119	1.1	46.7
		Annual thickness if *P. glacialis* RS sub-laminae are present	20.25 (9.1)	26	7.9	40.6
		P. glacialis RS sub-lamina thickness [1]	2.2 (1.4)	35	0.5	5.9
Dumont d'Urville Trough (MD03-2601) Neoglacial Hypsithermal	—	Annual thickness	21 (14)	10		
	T. antarctica RS	Annual thickness	46 (16)	6		
		T. antarctica RS sub-lamina thickness	0.371 (0.289)	8		
Iceberg Alley (NBP0101 JPC43B) Deglacial	*T. antarctica* RS	Annual thickness	21.59 (17.69)	223	1.04	99.05
		Annual thickness if *T. antarctica* RS sub-laminae are present	21.98 (16.16)	67	1.86	81.32
		T. antarctica RS sub-lamina thickness [2]	1.16 (1.70)	68	0.03	10.47
		Summer thickness	5.35 (5.45)	159	0.28	33.49
		Summer thickness if *T. antarctica* RS sub-laminae are present	5.74 (6.86)	46	0.33	33.49
		T. antarctica RS sub-lamina thickness if associated with top of summer lamina [3]	1.33 (2.04)	43	0.03	10.47
		Transitional lamina thickness	9.52 (9.28)	110	0.73	49.76
		Transitional lamina thickness if followed by *T. antarctica* RS sub-lamina	8.29 (4.49)	25	1.26	18.42
		T. antarctica RS sub-lamina thickness if associated with top of transitional lamina [4]	0.88 (0.81)	25	0.25	3.28

[1] 26 years have *P. glacialis* RS sub-laminae; 5 years have multiple sub-laminae

[2] 67 years have *T. antarctica* RS sub-laminae; 1 year has 2 sub-laminae

[3] 46 years have *T. antarctica* RS sub-laminae; in 43/46 years the sub-lamina is at the top of the summer lamina; in 3/46 years, the sub-lamina is within the summer laminae

[4] Four transitional laminae, overlain by *T. antarctica* RS sub-laminae, are followed by summer laminae associated with *T. antarctica* RS sub-laminae

Table 3

Location	Sub-lamina type	*P. glacialis* RS or *T. antarctica* RS abundance in lamina or sub-lamina types	Mean Abundance (standard deviation) / x 10^6 valves/g	No. of Measure-ments (n)	Minimum / x 10^6 valves/g	Maximum / x 10^6 valves/g	Relative Abundance (%) All/CRS-free
Mertz-Ninnis Trough (NBP0101 JPC10)	*P. glacialis* RS	*P. glacialis* RS abundance in summer mixed diatom lamina	6.9 (2.7)	5	3.9	9.5	0.38 / 2.29
		T. antarctica RS abundance in summer mixed diatom lamina	0 (0)	5	0	0	0 / 0.42
		P. glacialis RS abundance in *P. glacialis* RS sub-lamina	7.2 (3.9)	4	3.2	10.6	0.24 / 11.35
		T. antarctica RS abundance in *P. glacialis* RS sub-lamina	0 (0)	4	0	0	0 / 0
Dumont d'Urville Trough (MD03-2597)	*P. glacialis* RS	*P. glacialis* RS abundance in summer mixed diatom lamina	20.3 (9.9)	5	10.9	34.8	2.91 / 5.1
		T. antarctica RS abundance in summer mixed diatom lamina	2.4 (3.6)	5	0	8.6	0.39 / 0.81
		P. glacialis RS abundance in *P. glacialis* RS sub-lamina	53.9 (27.2)	3	33.5	84.8	7.08 / 15.48
		T. antarctica RS abundance in *P. glacialis* RS sub-lamina	6.7 (6.7)	3	0	13.4	0.89 / 3.16

Table 4

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Mean Hypsithermal surface temperature (°C)	0.79	1.58	0.56	-0.94	-1.55	-1.62	-1.61	-1.61	-1.63	-1.65	-1.53	-0.63
Mean Neoglacial surface temperature (°C)	0.68	1.59	0.63	-0.90	-1.54	-1.61	-1.61	-1.61	-1.63	-1.65	-1.58	-0.78
z value	2.79	-0.16	-2.11	-1.97	-2.05	-1.84	-0.18	0.55	0.22	-2.16	7.82	7.07
Significance level of difference between the mean surface temperatures	99%	none	95%	95%	95%	90%	none	none	none	95%	>99%	>99%
Mean Hypsithermal sea ice concentration (%)	0.29	0.25	0.33	0.53	0.80	0.88	0.88	0.87	0.83	0.76	0.58	0.41
Mean Neoglacial sea ice concentration (%)	0.28	0.24	0.30	0.50	0.79	0.88	0.89	0.88	0.85	0.77	0.59	0.41
z value	2.15	3.20	4.61	4.86	2.52	-0.53	-3.42	-3.72	-3.80	-2.76	-1.38	0.87
Significance of difference between the mean sea ice concentrations	95%	>99%	>99%	>99%	>98.5%	none	>99%	>99%	>99%	99%	none	none

Figure 1

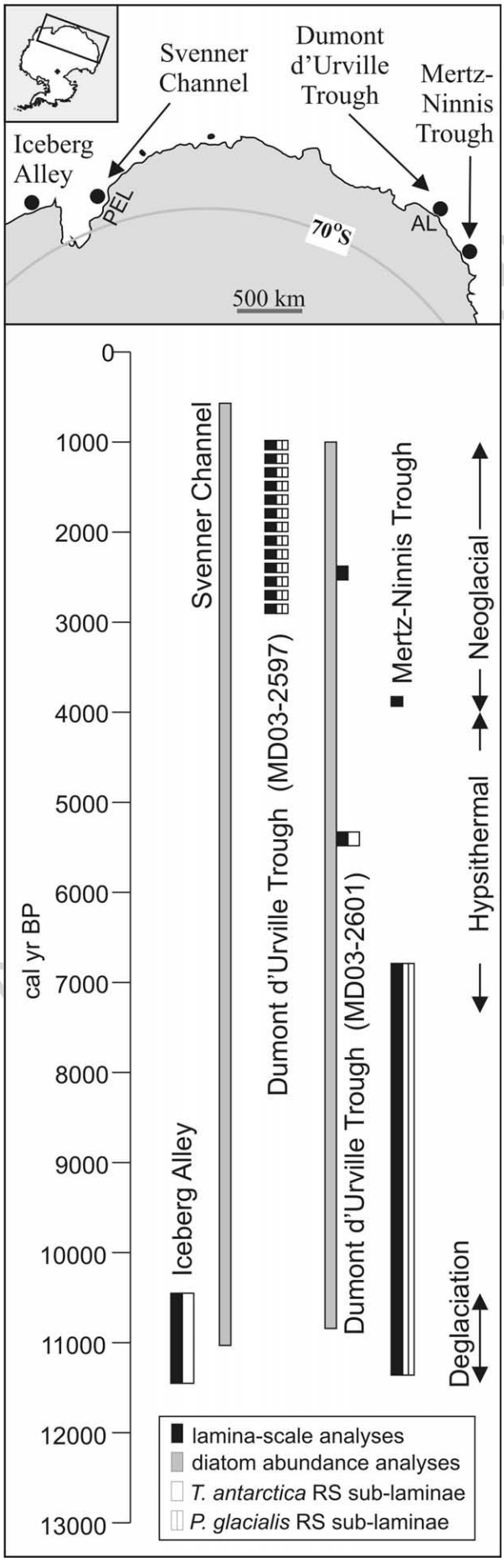

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Figure 2

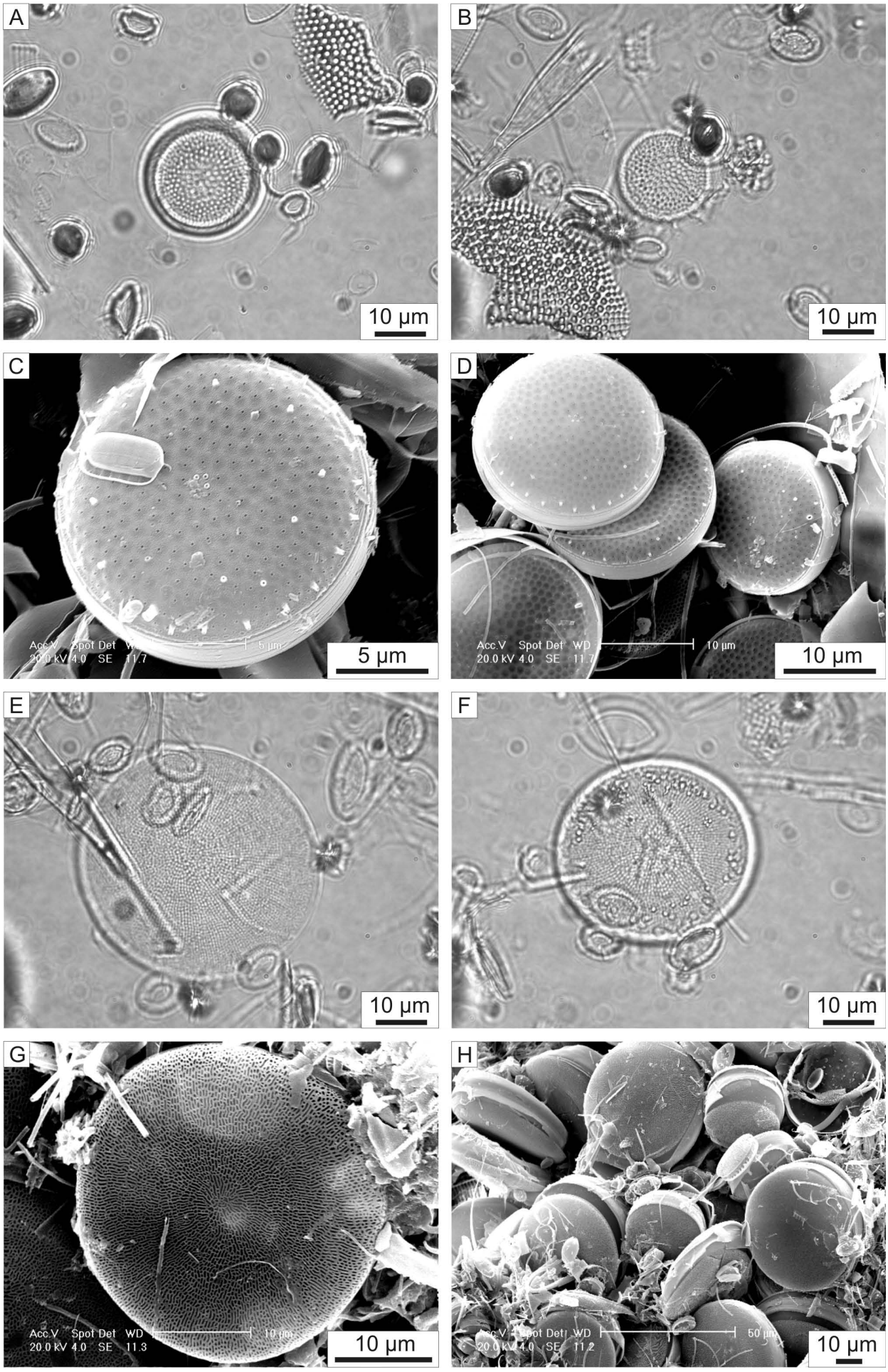

Figure 3

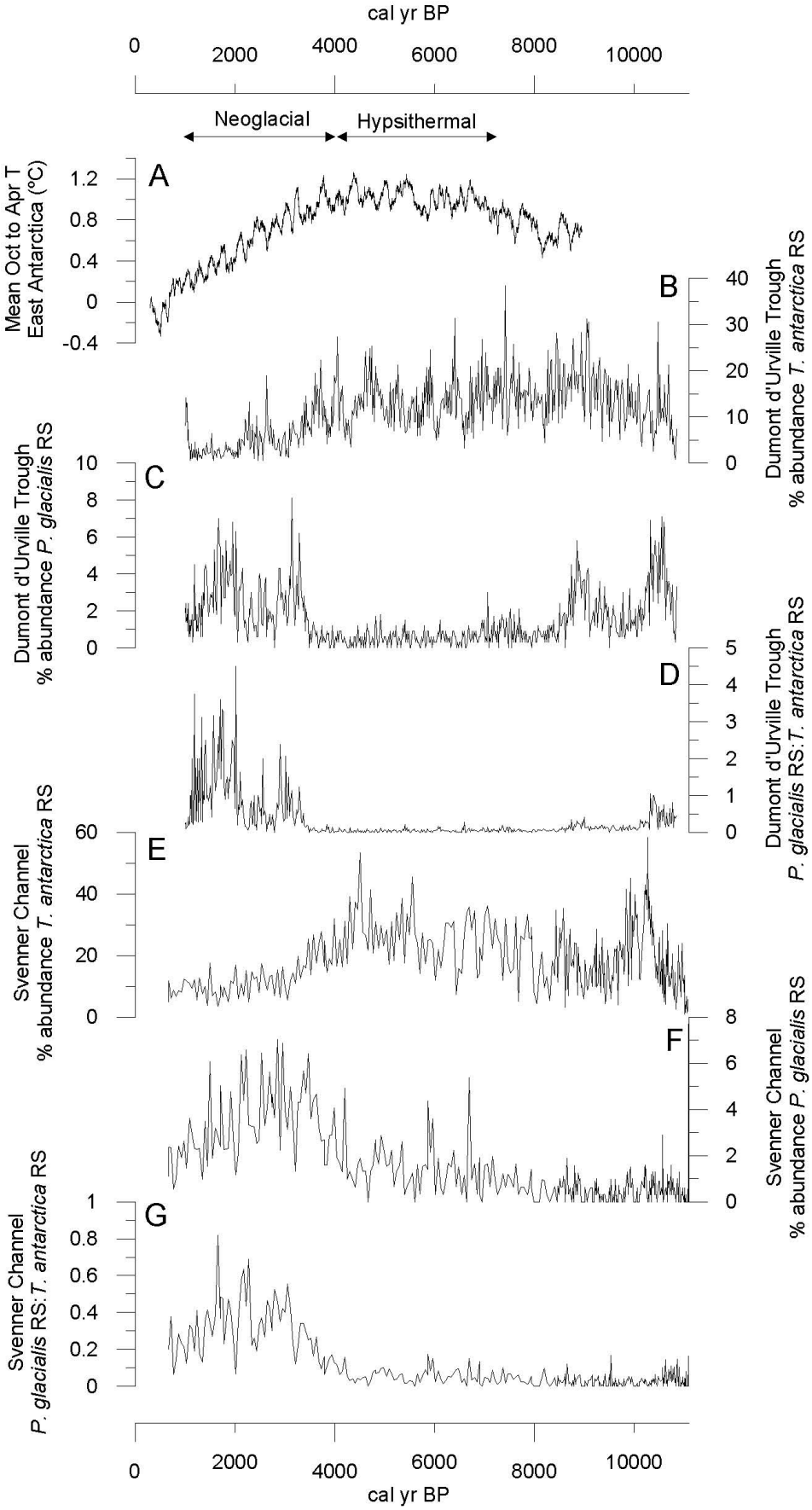

Figure 4